THE WATER ECONOMY OF SALAMANDERS: EXCHANGE OF WATER WITH THE SOIL

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Many species of amphibians spend their active periods at some distance from surface waters, and, consequently, cannot depend entirely upon ponds, pools, and streams for water to replace evaporative losses. These animals probably depend upon the water stored in the soil, and the availability of this water to them is an important parameter of their ecology.

Heatwole and Lim (1961) have shown that, at some water contents, the water in the soil was available to the salamander, *Plethodon cinereus.* They also showed that the lowest soil water level at which the salamander could withdraw moisture (the "absorption threshold") had the same moisture tension value in several soils. They thus introduced the moisture tension scale as a scale of the availability of soil water to salamanders.

In this study, I investigated the exchange of water between soil and salamanders in the soil, using six salamander species and a range of soil moistures. The following questions were investigated: (1) How does the rate of water exchange vary with the soil moisture? (2) What differences are there between different salamander species? (3) What variables other than the species and the soil moisture affect the exchange rates? (4) Can a salamander rehydrate fully in soil? With the data from these experiments, it is possible to predict the availability of water to these salamanders at any particular site.

Materials and Methods

The soil used was a homogeneous mixture of several local soils. Its characteristic curve, as determined on a porous plate apparatus (Soil Moisture Equipment Company; see Marshall, 1959, Ch. 2) is given in Figure 1. Lots of soil containing 10%, 6%, 4% and 1% water were packed into culture dishes. These lots provided a range of moistures from above field capacity (soil containg about 9% water) to air-dry soil (containing about 1% water).

The animals were dehydrated in air until they had lost approximately 15% of their initial body weight (this loss, expressed as a percentage of the initial weight, is the "dehydration deficit"). Each animal was then buried in a culture dish filled with soil at one of the four moisture contents. The animals were removed after six hours, and a soil sample was taken. Each salamander's bladder was emptied, and the salamander was then weighed to the nearest 5 mg. on a torsion balance (in the experiments with air-dry soils, the salamanders were not initially dehydrated, and were left in the soil only 2, 3 or 4 hours). The weight change

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over the six-hour interval was assumed to be due to water exchange, and was expressed as a rate [mg./(cm.^{2} × day)] where the surface area was calculated with Benedict's (1932) general formula:

$$(\text{Surface Area}) = 10\ (\text{Body Weight})^{2/3}.$$

The soil sample was dried for 48 hours at 105° C. The soil moisture was calculated from the change in weight. Figure 2 shows the relation between soil moisture and exchange rate for this initial 6-hour period.

Some of the animals which were losing weight were returned to the soil and exposed for an additional 12- or 24-hour period. The weight changes over this period were used to determine the variation in water loss with the length of the exposure period.

All the animals which gained weight during the first 6-hour interval were returned to the soil. These salamanders were removed for weighing at 24-hour intervals until they had stopped gaining weight. The peak weight attained,

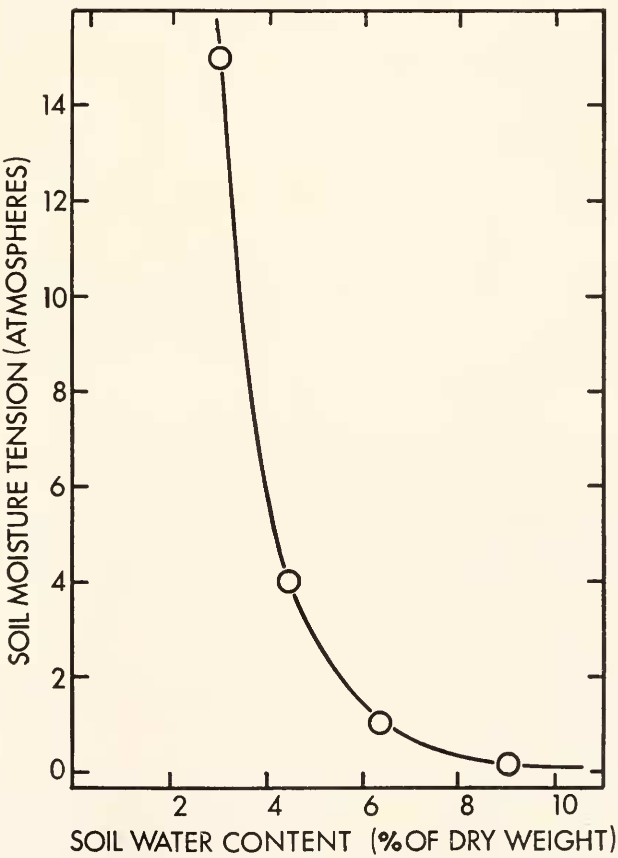

FIGURE 1. Characteristic curve of the soil used in the experiments. Each point is the mean of three values.

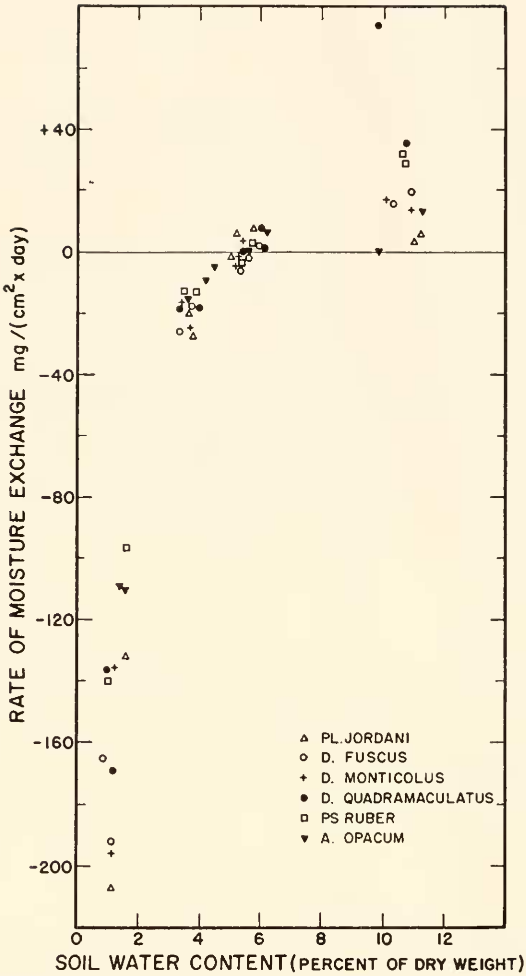

FIGURE 2. The relationship between soil water content and the rate of water exhange by six species of salamanders. The weights and dehydration deficits of the animals used in these experiments are given in Spight (1966a).

expressed as a percentage of the original weight, was the rehydration success of the animal.

All animals spent a final 48 hours in tap water. A weight increase during this period was assumed to indicate that the animals were unable to complete rehydration in soil.

Six species of salamanders were used in these experiments: the terrestrial, lunged *Ambystoma opacum,* and these lungless salamanders: *Desmognathus quadramaculatus,* from mountain streams; *D. monticolus,* from mountain stream banks; *D. fuscus,* from Piedmont streams and stream banks; *Plethodon jordani,* a forest floor form with no aquatic phase, and *Pseudotriton ruber,* a terrestrial form with an aquatic phase.

Results

Moisture tension and species as variables

The rate of water exchange with unsaturated soil is a function of the water content, and the function is the same for all of the species tested (Fig. 2).

The soil moisture tension is presumably a measure of water availability to salamanders, and, if Figure 1 is superimposed on Figure 2, it can be seen that the exchange rate is a function of the moisture tension. The moisture tension relationship will remain constant from soil to soil, and rates observed in these experiments, expressed as a function of the soil moisture tension, will serve as a basis for predicting performance in other soils. The water content allowing a particular exchange rate will, on the other hand, vary with the composition of the soil, and can be predicted for another soil only when the characteristic curve is available for that soil.

The range of moistures of critical importance to a salamander is the range about its absorption threshold, since it is only in soil above that threshold that a salamander can potentially remain in water balance. Within this range, the only variable which determines the rate and direction of water exchange over the six-hour measurement interval is the water content of the soil. The animals clustered about the 2 atm. (about 5%) point have a wide range of weights (1 g. to 10 g.) and dehydration deficits (8% to 20%) but all exchange water with the soil at rates solely dependent upon the water content of the soil (Fig. 2).

Additional variables in water exchange

Soil moisture was the only variable which affected the rate and direction of water flow between salamanders and soils when the soils had moisture tensions between 0.3 atm. and 15 atm. and when the measurement intervals were equal. In the saturated soils, however, the salamanders' rate of water uptake is correlated with both weight and dehydration deficit. The exchange rate by an individual salamander over a six-hour period in soil was also markedly different from that over a 12-hour period.

If the data from the two individuals of each species which rehydrated in saturated soil are compared, the differences between the members of each pair are correlated with differences in body weight and dehydration deficit. For examples, the larger of the pair of *D. fuscus* had the lower rate of gain, both animals having the same dehydration deficit. For the pairs of *D. monticolus* and *Plethodon jordani* of the same weight, the animal in each pair with the greatest dehydration deficit had the greatest rate of uptake. For pairs of salamanders of the species *Pseudotriton ruber* and *A. opacum,* the smaller animal had the greater deficit and absorbed water from the soil more quickly. The data for *D. quadramaculatus* are ambiguous. In all cases, for animals with similar dehydration deficits, the rates of rehydration in soil were well below the average rates of rehydration in water [rates in water ranged from 24 mg./(cm.^{2} $\times$ day) to 190 mg./cm.^{2} $\times$ day); see Spight, 1966b].

The rate of loss by salamanders to air-dry soil (by the 12 animals with the highest loss rates in Figure 2) is inversely correlated with the time the animals spent in the soil. The four animals which spent only two hours in soil had an average rate of loss of 190 mg./(cm.^{2} × day); all their rates fall within the range of rates of loss by animals which were dehydrated in room air [for 60% to 70% relative humidity at 20° C., animals lost 100 to 310 mg./(cm.^{2} × day) by evaporation to the air; see Spight, 1966a]. In contrast, animals which spent 3 hours or 4 hours in soils of the same water content averaged, respectively, 140 and 110 mg./(cm.^{2} × day).

The mediating influence of the soil is particularly prominent in the air-dry soils, for in these soils a small amount of water lost by a salamander to the surrounding soil will lower the tension of that soil markedly (note the slope of the characteristic curve in Figure 1 for soils containing less than 4% water). The mediation was also evident in the moist soils. When one individual spent successive intervals of 6 and 12 hours in the same soil, the loss rate was appreciably lower over the longer interval (Table I).

TABLE I

Rates of water loss by individuals to moist soils during successive periods of different lengths in the same soil

Species	Rate of water loss		Soil moisture %
	Hours 1 to 6 mg./ (cm.^{2} × day)	Hours 6 to 18 (mg./ (cm.^{2} × day)	
Desmognathus fuscus	−18.2	−13.8	3.71
D. monticolus	−16.4	−11.4	3.46
D. monticolus	−25.0	− 9.4	3.70
D. quadramaculatus	−18.6	−11.4	3.42
D. quadramaculatus	−18.5	− 8.9	4.00
Plethodon jordani	−19.9	−10.0	3.64
Plethodon jordani	−27.5	−10.5	3.78
Ambystoma opacum	−16.6	−13.0	3.62
Pseudotriton ruber	−12.9	− 8.3	3.58
Pseudotriton ruber	−13.1	− 8.6	3.91

Rehydration ability

The salamanders can complete rehydration in saturated soil, although the rate of gain is slow in comparison with rates of rehydration in water. Twelve animals attained 93.2% of their initial weights (SE = 0.6) from soils with 9% to 11% water, taking one to four days to complete the rehydration. These animals made no further weight gains during 48 hours in water.

Animals exposed to soils containing 5% to 6% water showed initial weight gains, but these soils dried below the absorption threshold before the animals were able to complete rehydration. These animals subsequently attained 92.4% of their original weights by rehydration in water (SE = 1.1, N = 12); this percentage is not significantly different from the percentage attained by the group of salamanders which were able to complete rehydration in soil ($P > 0.50$ that the difference has arisen by chance alone).

It is postulated that a salamander can complete rehydration in any soil from which it can gain any water, although it is doubtful that this can be shown in the laboratory, since it is extremely difficult to maintain soil at a precise moisture tension.

Discussion

Salamanders are found in both "wet" and "dry" communities, and species can be characterized by their "water requirements." Some species are wholly aquatic, others semi-terrestrial, and others wholly terrestrial. Investigators, including G. K. Noble (1931), have suggested that the distributions of different amphibian species might be correlated with specific differences in their ability to absorb water from various substrates. This study has shown that if the soil water at a particular site is available to a terrestrial species, it will also be available to a characteristically aquatic species. In other words, in spite of well documented differences in "water requirements," knowledge of the availability of water in the substrate of a habitat cannot be used to make predictions about which salamander species will be able to occupy that habitat. Salamanders thus present another example of Beament's (1961) generalization that, among closely related animals, even species from quite different habitats have only minor differences in their physiologies.

Salamanders can absorb water from soils with moisture tensions less than 2 atm. The meaning of this value in typical natural situations can be clarified by pointing out three particular points on the moisture tension scale. Soil is normally considered (1) to be at a tension of 0.33 atm. when the gravitationally-induced draining of a rain-wet soil is complete, and (2) to be at a tension of 15 atm. when a plant growing in the soil becomes permanently wilted. Van Bavel (1953) gives the third point (3): on non-irrigated crop land near Raleigh, N. C., during the average year there will be 20 days during which the soil moisture rises above 0.77 atm. (he considers this tension to be a stress level for agricultural plants). It may be seen, then, that salamanders can obtain water from agricultural land in North Carolina throughout most of the year.

Soil properties and moisture exchange

As the time the salamander spends in soil below the absorption threshold increases, the rate of water loss by the salamander to the soil drops. This rate drop is more prominent in the air-dry soils, but it is also evident in the wetter soils. These rate drops reflect the water conductance of the soil used, and a related phenomenon, the wetting front.

In unsaturated soils (soils with tensions greater than 0.33 atm.), a wetting front, a locally steep gradient of moisture content, is formed between a wet region and a drier region (Klute, 1952). The gradient is such that in very dry soil there may be no movement of liquid water from a wet region (at about field capacity) to an adjacent, very dry region (air dry; Bodman and Colman, 1944).

As water is lost by the salamander to the soil, it is absorbed by the immediately adjacent soil, and a wetting front is formed. The water lost by the salamander accumulates between the salamander and the edge of the wetting front. In this zone, the humidity increases with the accumulation of water; thus the accumulated water lowers the humidity gradient from the salamander to the adjacent soil, and the evaporation rate of the salamander decreases.

Soil water at some moisture tensions is available to many salamander species, and the availability of the soil water at a particular site to a salamander can be predicted. With this information, it is possible to approach old problems, such as "does water act as a limiting factor in the distribution of salamanders," and "what are the water problems of hibernating salamanders?" These experiments have not shown that anurans have the same absorption threshold as do these urodeles. Such a demonstration would make an interesting future study, and would lead directly to the solution of the problem, "where do desert toads get their water?"

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Summary

Specimens of six salamander species were exposed to different soil moistures, and rates of water exchange were calculated from the changes in weight observed. Soil water was available to these salamanders in soils with moisture tensions between 0 atm. and 2 atm. At these tensions, salamanders could rehydrate fully, and can therefore be expected to remain in water balance in any soil with a tension in this range. The measurements should be useful in determining the suitability of habitats for salamanders. The rate of water exchange between the salamander and the soil was a function of the soil moisture tension. The rate of uptake from saturated soils was correlated with the body weight and the dehydration deficit of the salamanders. There were no differences in rate of exchange or in absorption threshold between the different species. These characteristics of water exchange between salamanders and soil are related to the properties of the soil.

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